

STUDIES ON THE TETRACLITIDAE  
(CIRRIPEDIA: THORACICA): A PROPOSED  
NEW GENUS FOR THE AUSTRAL SPECIES  
*TETRACLITA PURPURASCENS BREVISUTUM*

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ABSTRACT. — *Epopella* gen. nov. is proposed for the Auckland Islands species *Tetraclita purpurascens* forma *brevisutum* Broch, 1922, a solid-walled tesseroporan. *Elminius plicatus* Gray and *E. simplex* Darwin are assigned provisionally to this new genus on the basis of morphological similarities. *Epopella*, containing the most primitive tetraclitids, is inferred to have evolved during the early Paleogene, and it is from this group that *Tesseropora* and later tesseroporans are derived.

RESUMEN. — *Epopella* gen. nov. esta propuesto para el especies de las Islas Auckland *Tetraclita purpurascens* forma *brevisutum* Broch, 1922, un tesseroporan que tiene una pared sólida. *Elminius plicatus* Gray y *E. simplex* Darwin son asignados provisionalmente a este género nuevo en el base de semejanzas morfológicas. *Epopella*, conteniendo las tetraclitids más primitivas se infiera que ha evolucionada durante del Paleógena, y es de este grupo que *Tesseropora* y tesseroporans más tarde están derivado.

Knowledge of the tetraclitid fauna of Australia, Tasmania, New Zealand, and the islands comprising the Antipodean Province is limited. Aside from the taxon Broch (1922: 337) described as *Tetraclita purpurascens* forma *brevisutum*, the following species are known from this region: *Tesseropora rosea* (Darwin, 1854: 335; Linzey, 1942: 280; Pope, 1945: 366; Wisely and Blick, 1964: 166), *Tetraclita vitiata* (Stephenson, 1968: 51), and *Tetraclitella purpurascens* (Darwin, 1854: 337; Linzey, 1942: 279; Foster, 1967a: 83; 1967b: 35).

*Tetraclita purpurascens* forma *brevisutum* was collected by the Th. Mortensen Pacific Expedition (1914-1916) on Auckland Island, the largest of several islands in the Auckland Islands Group (Fig. 1), and more recently it has been found on Rose Island. This species has neither been reported nor found in collections from any other locality and appears to be endemic to the Auckland Islands. Unfortunately, there is little known about the ecology of this tetraclitid.

Hiro (1939: 275) noted differences in the opercular plates of *T. purpurascens* forma *brevisutum* that indicated it was not closely related to the nominate subspecies. However, he failed to indicate the affinities of this form to other tetraclitid groups. In re-examining the type specimens I noted several salient wall structures that readily characterize this taxon at the generic and specific level and suggest that its affinities are to the tesseroporan rather than to the tetraclitellan lineage (Ross, 1969: 238). Consequently, the "forma" *brevisutum* is elevated to specific rank and the genus *Epopella* proposed for it and two other related species.

FAMILY TETRACLITIDAE Gruvel

*Remarks.* — The familial diagnosis presented earlier (Ross, 1969: 238) is emended to include those species that lack an inner lamina and have an outer lamina permeated by cuticular chitin.

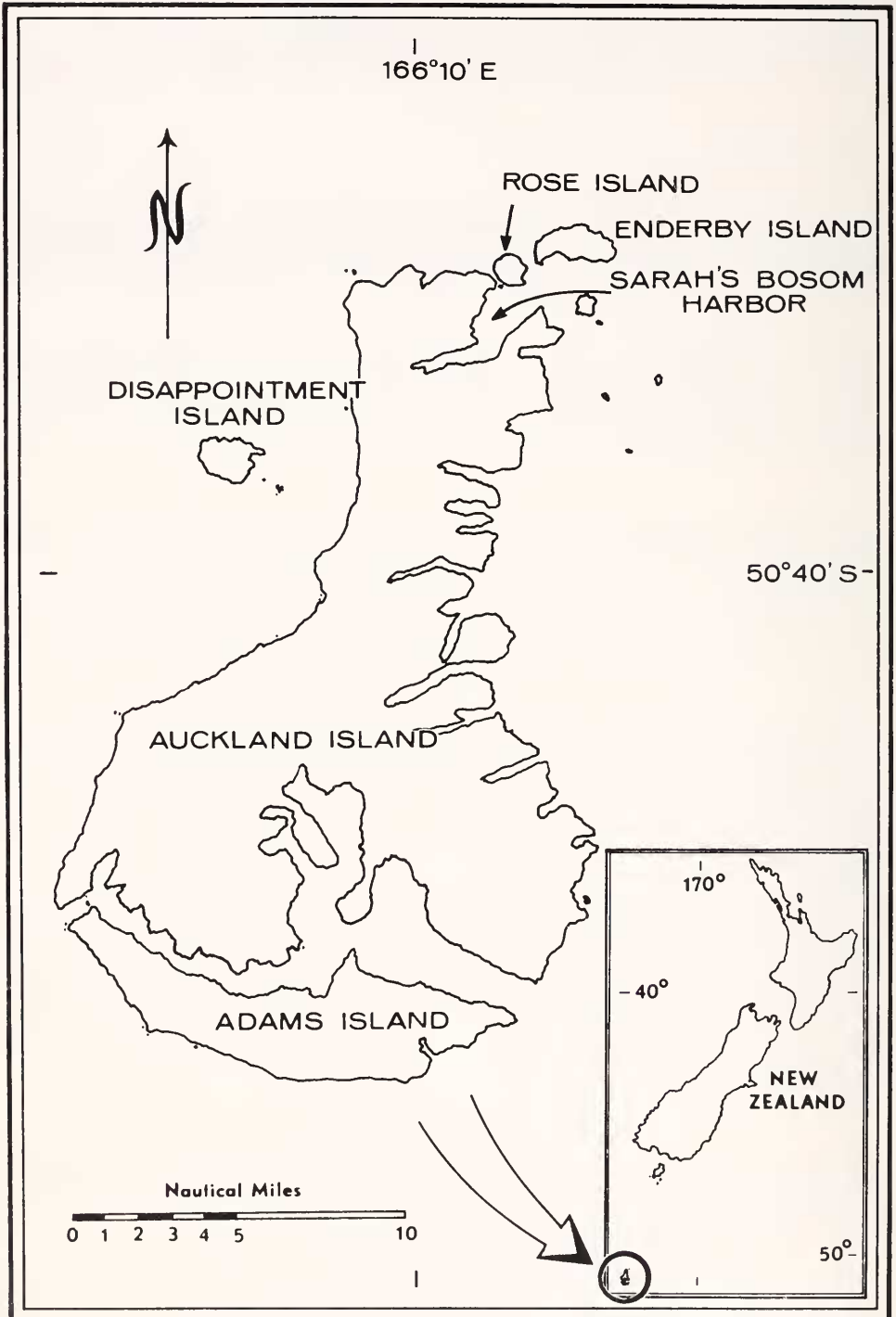


Figure 1. Map of Auckland Islands Group, and its position relative to New Zealand (inset). The known occurrences of *Epopella breviscutum* are Sarah's Bosom Harbor and Rose Island.

## KEY TO GENERA OF THE TESSEROPORAN GROUP

1. Parietal tubes uniformly distributed in one row . . . . . 2
1. Parietal tubes uniformly distributed in more than two rows, or lacking . . . . . 3
2. Parietal tubes bearing transverse septa; scutum lacking depressor muscle crests (1 sp., eastern Pacific, Pliocene) . . . . . *Tesseroplax*
2. Parietal tubes lacking transverse septa; scutum bearing depressor muscle crests (5 spp., Indo-West Pacific, Recent; Italy, Oligocene) . . . . . *Tesseropora*
3. Inner lamina present; longitudinal septa continuous; sheath adpressed, basal margin not depending (19 spp., tropical, warm temperate, cosmopolitan, Pliocene to Recent) . . . . . *Tetraclita*
3. Inner lamina absent; longitudinal septa discontinuous; sheath free with basal margin depending (3 spp., southeast Australia, New Zealand, Recent) . . . . . *Epopella*

**Epopella** gen. nov.

*Definition.* — Shell large, conic; compartments may or may not be discrete; parietes effectively solid, permeated with cuticular chitin, and commonly discontinuous plates or longitudinal lamina depend from inner surface; radii non-tubiferous, narrow or obsolete; basis membranous; scutum triangular, higher than wide, bearing crests for depressor muscles; tergum narrow, spur not well separated from basi-scutal angle, truncate basally; mandible with 4 teeth, basal comb, and spine-like inferior angle; maxilla I with 10-16 spines comprising medial cluster of cutting edge.

*Type species.* — *Tetraclita (Tetraclita) purpurascens* forma *breviscutum* Broch, 1922, Recent, Auckland Island.

*Etymology.* — Named in honor of Elizabeth C. Pope, the Australian Museum, in recognition of her many contributions to the Cirripedia of the Australian region.

*Epopella breviscutum* (Broch)

*Tetraclita (Tetraclita) purpurascens* forma *breviscutum* Broch, 1922: 337, figs. 71, 72.

*Tetraclita (Tetraclitella) purpurascens* forma *breviscutum*: Hiro, 1939: 275.

*Material.* — Rose Island, Auckland Islands; intertidal; J. C. Yaldwyn, coll., January, 1963; 2 dried specimens lacking appendages and body; in collections of Dominion Museum, Wellington, New Zealand.

Sarah's Bosom Harbor (Port Ross), Auckland Island, Auckland Islands; under stones at low tide; Th. Mortensen Pacific Expedition, November 26, 1914; 5 complete specimens; in collections of Universitetets Zoologiske Museum, Copenhagen, Denmark.

*Supplementary Description.* — Shell low, conic; grayish-white; parietes deeply eroded; growth ridges discernible along basal margin only; orifice pentagonal with peritreme eroded; radii extremely narrow or obsolete, with articular surfaces weakly crenate; compartments weakly articulated when not secondarily fused; no inner lamina; longitudinal septa discontinuous basally, not fused, forming separate, smooth, depending plates (Fig. 2d), in general appearance not much unlike that of *Chelonobia testudinaria*; basal margin of sheath free, depending (Fig. 2d). Basis membranous. Measurements (in mm.) of the lectotype (26-XI-14D), paralectotypes (26-XI-A-C,E), and specimens from Rose Island (spec. F, G) are presented in Table 1.

External surface of opercular plates deeply eroded (Fig. 2a, b). Scutum triangular, commonly slightly higher than wide, articular ridge sinuous, about 2/3 length of tergal

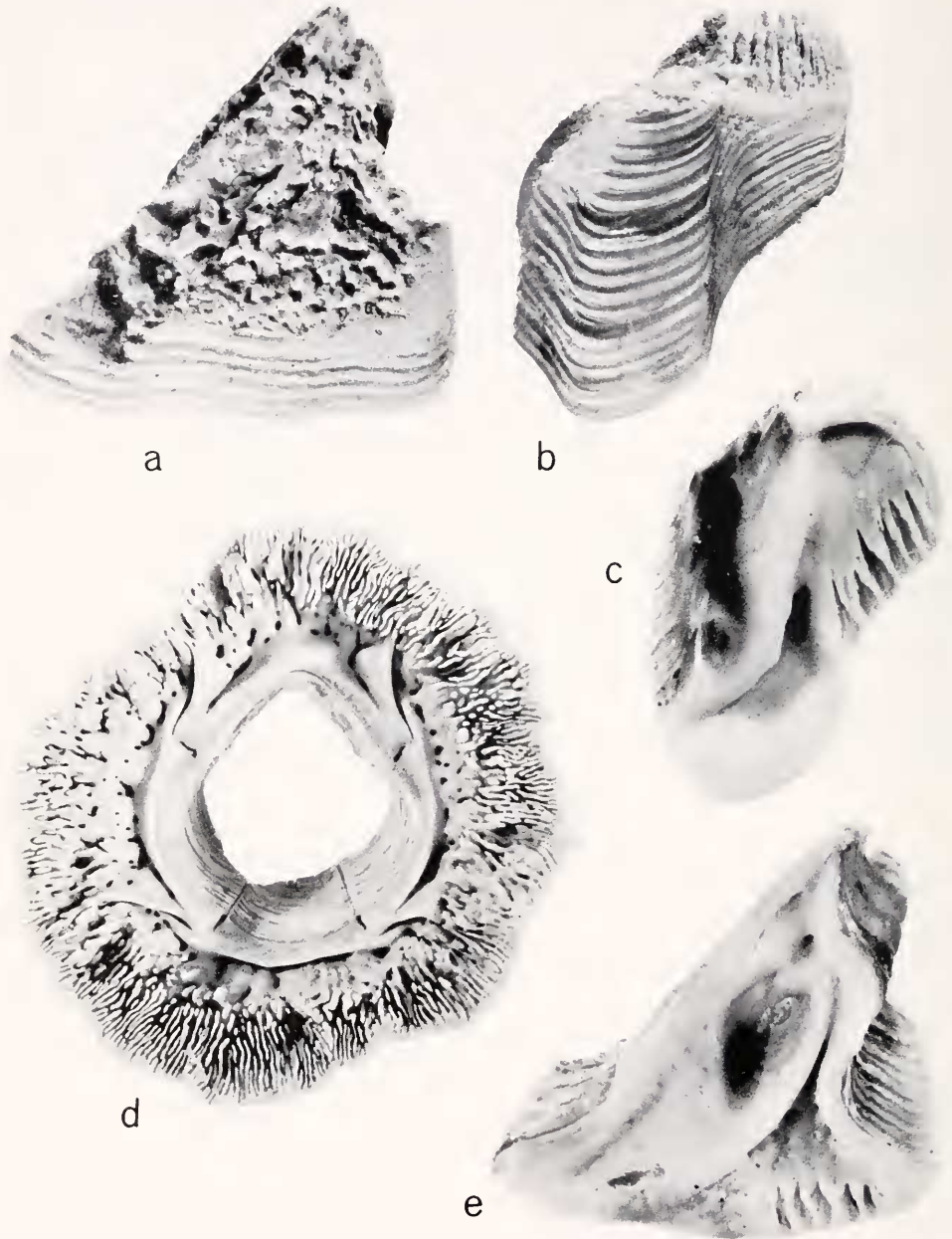


Figure 2. Shell and opercular plates of *Epopella breviscutum*. a, external view of scutum; b, external view of tergum; c, internal view of tergum; d, basal view of shell; e, internal view of scutum. Lectotype (26-XI-14D), a-c, e; paralectotype (26-XI-14A), d.

margin; adductor ridge erect, undercut, fused apically with articular ridge and extending nearly to basal margin; adductor muscle depression ovate, deep; 3-4 crests for rostral

depressor muscle, low, thin, partially hidden by infolding of occludent margin; 4-5 crests for lateral depressor muscle, high, broad, clearly exposed; overall surface of plate pitted (Fig. 2c).

Tergum higher than wide, apically eroded; external longitudinal furrow open, shallow, extending to base of spur; spur truncate basally, width more than 1/2 that of basal margin; articular ridge erect or inclined, undercut along basal portion; articular furrow broad and deep; 5-7 crests for depressor muscles, short, broad, erect, bearing close-spaced, thin, lateral extensions (Fig. 2c).

Table 1. *Measurements of Individual Specimens*

Specimen	Shell			Opercular Plates			
	C-R Dia.	Width	Height	S. H.	S. W.	T. H.	T. W.
<i>Auckland Id.</i>							
26-XI-14 A	29.9	29.2	14.4	9.4	8.7	8.3	5.1
26-XI-14 B	31.1	26.9	12.2	8.3	9.1	8.1	5.3
26-XI-14 C	31.0	30.9	14.3	10.1	9.4	8.7	4.9
26-XI-14 D (lectotype)	28.7	25.9	14.8	9.1	9.2	8.4	5.1
26-XI-14 E	32.9	31.4	12.7	8.2	10.2	8.9	5.2
<i>Rose Id.</i>							
F	16.8	19.4	9.4	7.8	7.2	6.4	4.8
G	16.1	18.5	10.8	6.8	6.5	5.1	4.8

Crest of labrum thick, heavily chitinized, with shallow medial notch (Fig. 3f); multidenticulate, 22-39 simple teeth along crest and in notch (Fig. 3g); short soft setae along crest and commonly between the teeth.

Palps bluntly rounded distally; superior margin concave, basal convex; distal setae 1/2 longer than superior; both bipinnate.

Mandible with 5 teeth including inferior angle (Fig. 3a); teeth 2-4 with subsidiary cusps; superior slope of tooth 4 smooth; inferior angle coarsely serrate, 28-42 overlapping, narrowly triangular teeth.

Maxilla I deeply notched subapically (Fig. 3c); spines along cutting edge in 3 clusters; 2 long, stout and 4-6 short, slender spines above notch; 10-16 long or short slender spines medially; 7-15 very short and slender spines basally.

Maxilla II taller than broad (Fig. 3e); anterior margin bilobate; basal lobe covered with cluster of pustules along anterior border.

Rami of cirrus I grossly unequal in length (Fig. 4a); posterior ramus about 1/2 length of anterior ramus. Rami of cirrus II either essentially equal in length or inner ramus slightly shorter; intermediate articles of both rami squat, slightly protuberant; setae on both rami coarsely bipinnate, not comb-like. Rami of cirrus III antenniform (Fig. 4d); outer ramus approximately 3/5 length of inner ramus; basal segments of both rami armed with comb-setae lacking basal guards (Fig. 4e). Cirri IV-VI essentially equal in length with equal rami; 3-5 short, slender setae at each articulation along greater curvature of intermediate articles; a single row of ctenae occurs along lateral face immediately below articulation; commonly 4 pairs of setae on cirri IV-V, and 3 on cirrus VI (Fig. 4f); at base of and between each major pair of setae is a cluster of 4-9 long bristles. Cirral counts for the specimens in the type lot are summarized in Figure 5.

Intromittent organ annulated throughout its length, and sparsely covered with short



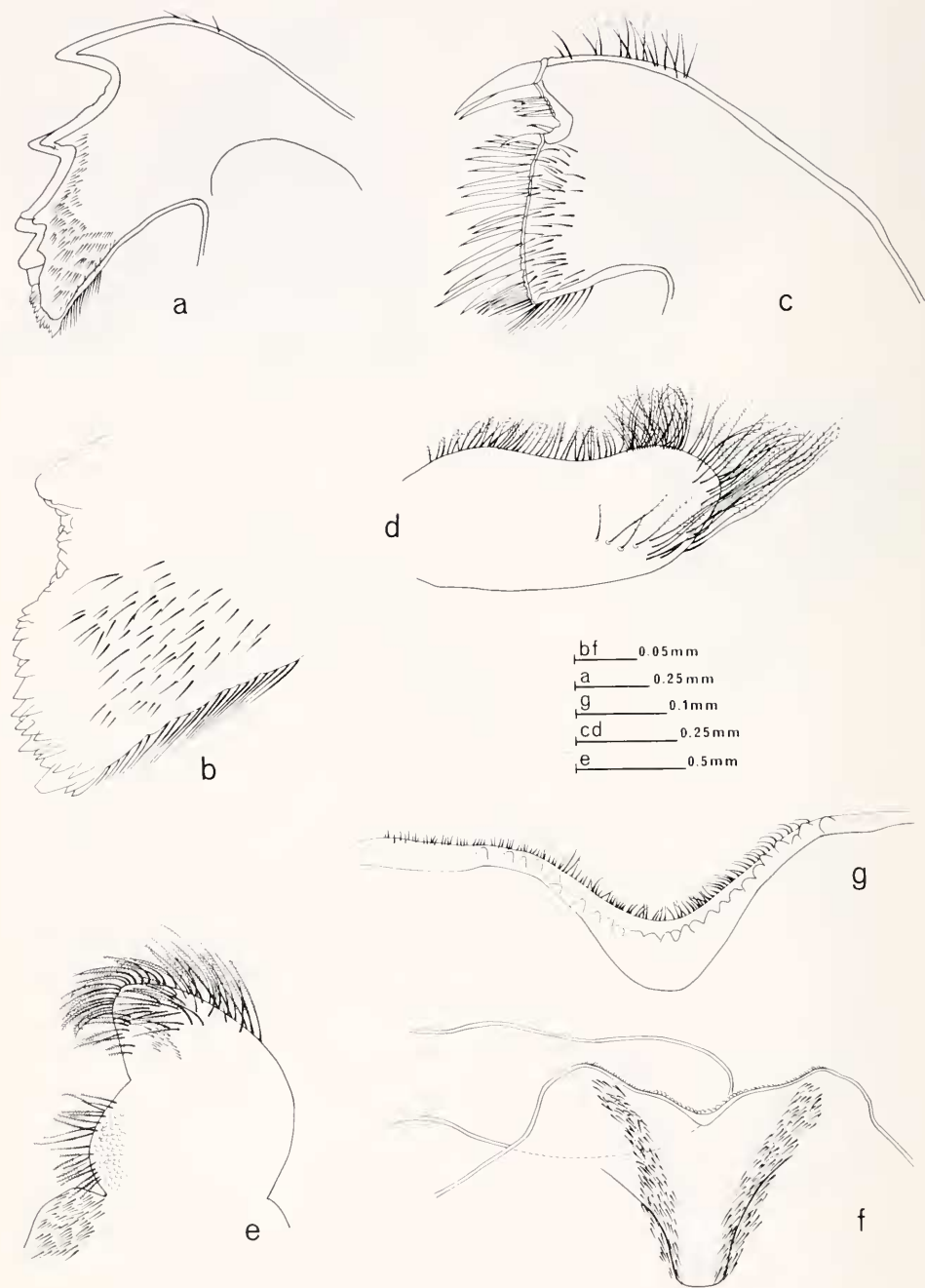


Figure 3. Trophi of *Epopella breviscutum*. a, mandible; b, enlarged view of inferior angle of mandible in fig. a; c, maxilla I; d, palp; e, maxilla II; f, labrum and palp; g, enlarged view of labral crest. Lectotype (26-XI-14D), a-e, g; paralectotype (26-XI-14B), f.

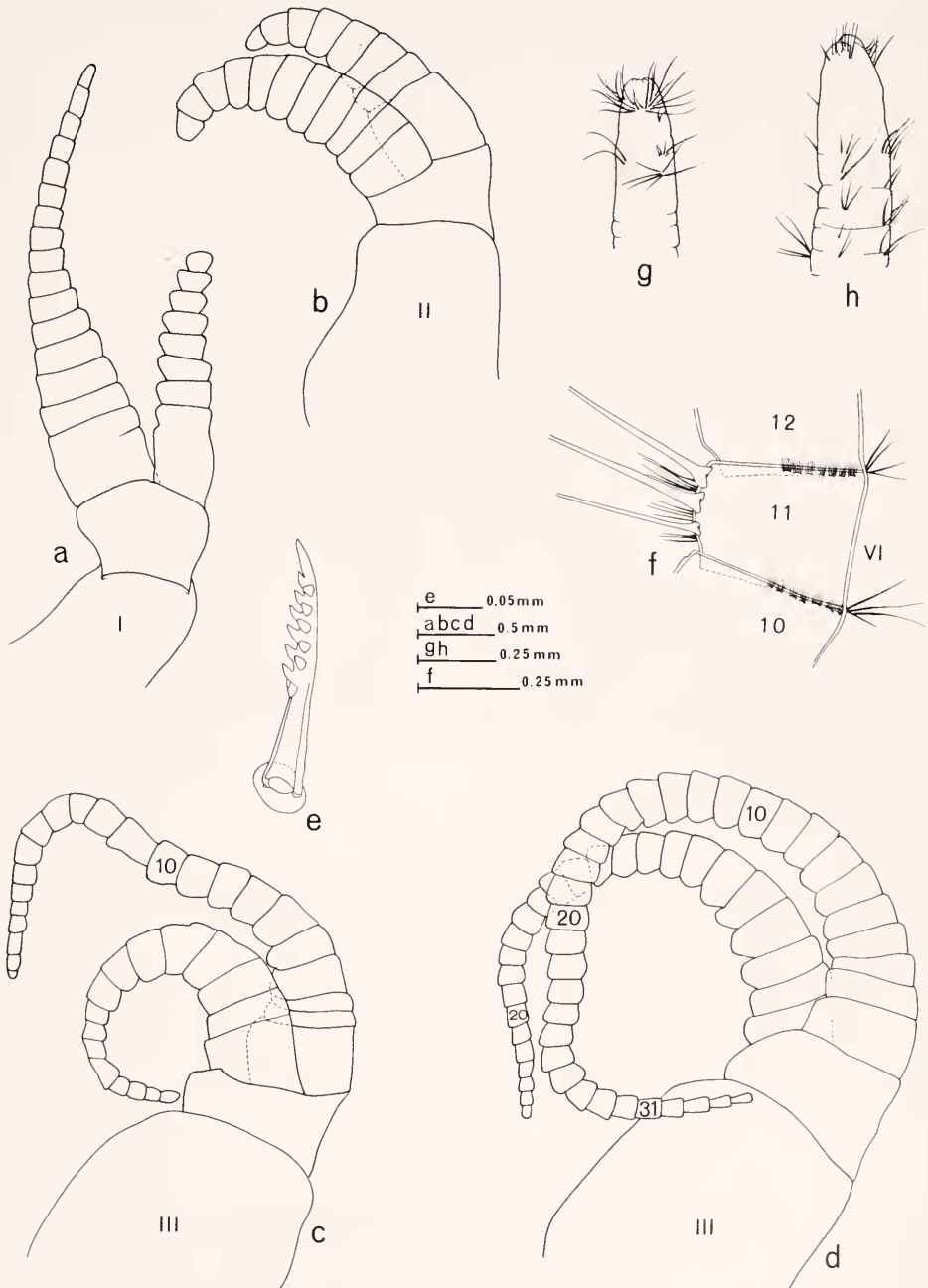


Figure 4. Thoracic appendages of *Epopella breviscutum*. a, left cirrus I; b, right cirrus II; c, right cirrus III; d, left cirrus III; e, comb seta from segment 5 of outer ramus of left cirrus III; f, intermediate segment of right outer ramus of cirrus VI; g, h, distal extremity of intromittant organ. Lectotype (26-XI-14D), b, c, f; paralectotypes, a, d, e, g-h (e, g, d = 26-XI-14C; a = 26-XI-14A; h = 2X-XI-14B).

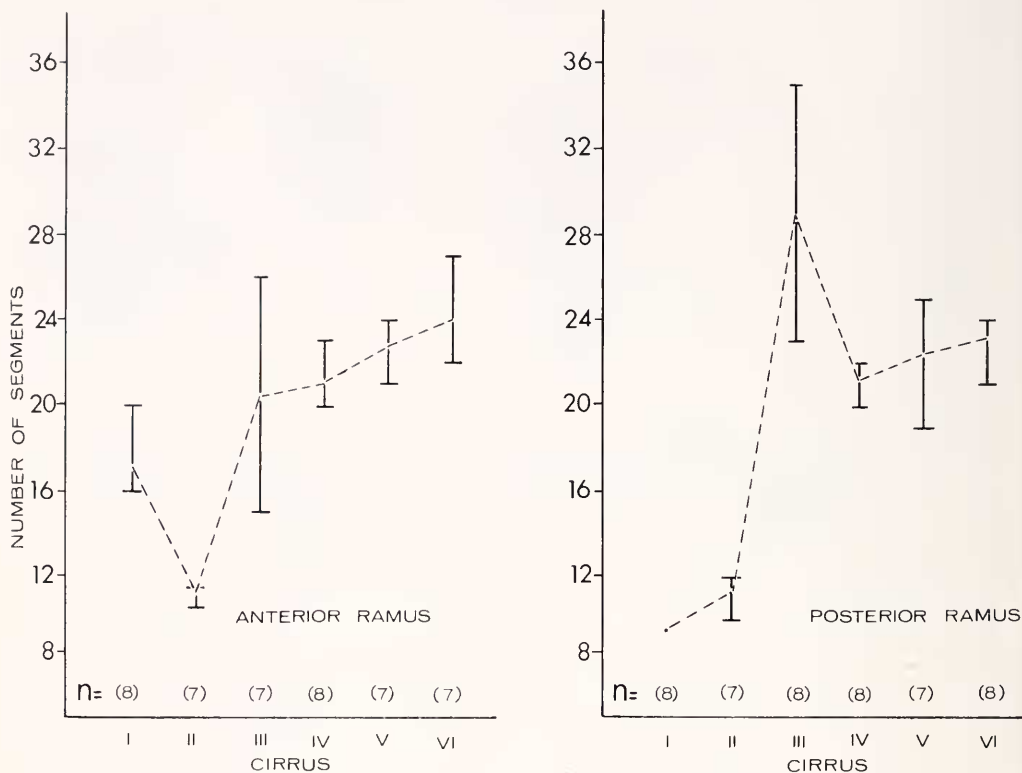


Figure 5. Graph of range (vertical line) and mean values (dotted line) for cirral counts of anterior ramus (left) and posterior ramus (right) of *Epopella breviscutum*.

bristles; distal extremity bears two large separate clusters of long setules (Fig. 4g).

Embryos in mantle cavity average  $0.10 \times 0.22$  mm. Stage I nauplii in mantle cavity average  $0.12 \times 0.20$  mm.

*Remarks.* — Broch illustrated the opercular plates and trophi of *breviscutum*, but failed to select a holotype. Because the specimen or specimens he figured are no longer available, the specimens here figured (opercular plates, figs. 2a-c, 3; trophi, figs. 3a-e, g; cirri, figs. 4b, c, f) are designated the lectotype (26-XI-14D), and the remaining specimens, of which I have seen 4, are designated paralectotypes (26-XI-14A-C, E).

#### DISCUSSION

Monometric shell growth, non-tubiferous and narrow or obsolete radii, and the orifice enlarged by attrition rather than diametric growth clearly establish *E. breviscutum* as a member of the tesseroporan group (Ross, 1969: 238).

The space between the inner and outer lamina in *Tetraclita* is filled with a network of continuous longitudinal septa, which in effect create longitudinal tubes. These are more or less uniform in section, and occur in rows with the smallest and shortest tubes parallel to the outer lamina. In *Tesseropora* and *Tesseroplax* there is basically but one row of these tubes. *Epopella breviscutum* lacks an inner lamina, and thus is effectively solid walled. A



non-tubiferous or solid wall characterizes the geologically earliest chthamalids and balanids (Ross, 1965: 61; Ross and Newman, 1967:4; Newman, Zullo and Wainwright, 1967: 167). In the tesseroporan lineage, I interpret the evolutionary trend then as having been from a solid walled form with diametric growth (Ross, 1969: 240) to a solid walled form with monometric growth, such as *E. breviscutum* or an earlier related species, to *Tesseropora* with a single row of parietal tubes and not uncommonly secondary tubules, and terminating with *Tetraclita*. *Tesseroplax*, also with a single row of tubes, is an early derivative of *Tesseropora*.

Much confusion exists over the systematic position of *Eliminius*, largely because certain of the included species are morphologically similar to the Balanidae on one hand and to the Tetraclitidae on the other (Darwin, 1854: 346). Those similar to the Balanidae have a deeply notched or incised labrum (Moore, 1944: pl. 46), and an intromittent organ bearing a basidorsal point (Nilsson-Cantell, 1930: 225). Those similar to the Tetraclitidae have a shallow or slightly notched labrum (Broch, 1922: 341-342), lack the basidorsal point, have complex setae on cirrus III (lacking in the Balanidae) that exhibits antenniformy (Moore, 1944: 328), and there are gross similarities in the opercular plates. Additional morphological characters, especially in the shell, as noted below, strengthen the inference that at least two species of *Eliminius*, namely *E. plicatus* Gray and *E. simplex* Darwin, are tetraclitids rather than balanids. The criteria for forming this group are supported by the distribution of the species involved, all three occurring within the southeastern Australia-New Zealand region.

The parietal plates in *E. breviscutum* are complex, not only because they are a laminate of calcareous and chitinous materials, but because the inner surface of the wall develops an elaborate irregular series of depending ridges or longitudinal septa. These undoubtedly impart rigidity and strength to the wall and provide a broad base of attachment and vertical support, much as in *Emersonius* and *Chelonobia* (Ross and Newman, 1967: 16). The internal structure of the parietes in *E. plicatus* is much like that of *E. breviscutum*, but in *E. simplex* the chitinous material occurs in a row of equidistantly spaced thin columns instead of continuous ribbons.

In *E. breviscutum* irregularly scattered between the depending ridges are narrow tubules that in section are either oval, circular, or irregular. Similar surficial depressions occur in *E. plicatus*, *E. simplex*, *Tesseropora* (at the tips of the secondary longitudinal septa), *Tetraclita* (see Pilsbry, 1916: 252) and not uncommonly in *Chthamalus*. Since *Epopella* lacks an inner lamina these "tubules" are not homologous with the parietal tubes or secondary tubules of other tesseroporans. The functional significance of these tubules and depressions remains unknown.

Secondary calcification of the parietal tubes in tesseroporans aids in maintaining the shell in environments where it is subjected to abrasion or corrosion. The shell in *Tesseroplax* is strengthened by apical filling of the parietal tubes, much as in *Tesseropora* and *Tetraclita*, and by the formation of transverse septa in the basal portion. In *Epopella*, deposition of a layer of calcium carbonate between the youngest series of longitudinal septa serves the same function. Henry (1957: 36) has suggested that in *Tesseropora pacifica* the shell is reinforced through development of elaborate, hollow, spinous processes that extend into the parietal tube cavities, but further work is needed to substantiate this.

In the Balanomorpha there has been selection both for structural reinforcement of the shell (Darwin, 1854) and for the development in deep water forms of a protective mechanism against boring organisms (Newman and Ross, in press). However, *Epopella* and other tesseroporans in general differ from these deep water forms in having a relatively much thicker and more complex wall. The development of a thick, laminated shell in the

tesseroporans is probably an adaptation for the rigors of the intertidal zone (cf. Paine, 1966).

There is a considerable interval between the earliest known occurrence (Recent) of the evolutionary more primitive *Epopella* and of the more complex *Tesseropora* (Oligocene). Thus the *Epopella* lineage must be significantly older than the fossil evidence indicates, a conclusion that is also suggested by the morphologically complex shell of *E. breviscutum*. Therefore, it seems probable that the origin of the tetraclitids should be sought in rocks dating from the Eocene if not the Paleocene or Cretaceous.

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